The Impact of Logging on Woodland Caribou (*Rangifer tarandus caribou*): A Literature Review

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TABLE OF CONTENTS

TABLE OF CONTENTS i

INTRODUCTION 1

CARIBOU ECOLOGY 3

HYPOTHESES FOR THE DECLINE OF WOODLAND CARIBOU 6

Hypothesis I: Food Limitation 7

Lichen Biology 9

Environmental Impact of Logging on Lichen Growth . . 11

Caribou Behaviour in Relation to Logging 13

Hypothesis II: Increased Predation and Human Harvest 17

Predator-prey Theory 17

Wolf-caribou Association 21

Human Harvest 22

Hypothesis III: Parasitic Infection Due to Faunal Changes 23

TWO PROVINCIAL CUTTING PROPOSALS 25

RECOMMENDATIONS 30

ACKNOWLEDGEMENTS 35

APPENDIX I 36

APPENDIX II 39

BIBLIOGRAPHY 40

INTRODUCTION

Woodland caribou (Rangifer tarandus caribou (Gmelin)) inhabit lichen-rich areas of the boreal forest. This fire-driven ecosystem is interspersed with bogs, muskegs, lakes and rivers. Woodland caribou numbers in Manitoba are estimated to be 4,500 animals and are primarily in scattered groups (comprising of 30-50 individuals in a band) except for a herd of 1,500 animals on the Hudson Bay Lowlands. Recreational and subsistence use of woodland caribou in Manitoba is insignificant compared to other big game species.

Historically, woodland caribou inhabited southeast Manitoba and ranged south into Minnesota. Today, due to development activities over the years, caribou no longer occupy these historic ranges. The last resident herd of woodland caribou in southern Manitoba (Appendix 1) occurred in Whiteshell Provincial Park in the 1950's.

A number of areas encompassing woodland caribou range in Manitoba are being or are destined for timber extraction activities. There is a lack of definitive studies examining the impact of logging on woodland caribou and therefore it becomes necessary to extrapolate from other studies on this continent and abroad to identify the impacts and to derive applicable management strategies. Mahoney (1980:35) cautions that because

> "caribou demonstrate varying responses to a given stimulus under different environments, one is not free to assume on the basis of experience with a given herd in a given area that similar responses will be generated in another group of animals elsewhere."

Logging activities may act in such a way that they bring together in one location at a given time all of the negative factors influencing woodland caribou and thus act as a (catalyst) to initiate reduction of caribou populations (Darby 1985 pers. comm.). In other words, the removal of preferred caribou habitat reduces the space available to caribou to separate themselves from predators, other prey and man.

The purpose of this paper is to present many of the existing views and (often conflicting) hypotheses held by biologists on the impact of logging on woodland caribou and to devise timber harvest guidelines applicable to the boreal forest region of the Canadian shield in Manitoba. These recommendations are intended as interim proposals until specific ones can be developed (following testing and refinement) for each woodland caribou herd.

CARIBOU ECOLOGY

Caribou belong to the deer family (Cervidae) in the Order Artiodactyla. They are unique in that both males and females commonly have antlers and can be further described to be an even-toed ruminant with a four compartment stomach. At present, five subspecies of caribou are recognized in North America (Bergerud 1978b).

Caribou have a low reproductive potential compared to other cervids in North America (Bergerud 1974). Caribou commonly reach puberty at 29 months and have their first calf at 3 years of age (Bergerud 1971, Dauphiné 1976). If nutrition is especially favorable some 17-month-old animals come into estrus and if the diet is especially poor some animals may not breed until 41 months of age (Dauphiné 1976). Since caribou seldom twin, the birth rate tends to equal the pregnancy rate, which averages 82% for mature females in North American herds (Bergerud 1980). Parturition rates appeared to vary little among years in established Newfoundland herds (Bergerud 1971). Gauthier (1984), in a literature search, could find no correlation between percent males in herds and parturition rates of parous females ($\geq$2 years of age) based on six North American herds. Thomson (1977; vide Gauthier 1984:3) studied wild reindeer and concluded that "even with a severe reduction in number of adult males, reproductive rates remain reasonably high." This suggests that "caribou have little phenotypic plasticity in their reproductive adaptive strategy that might vary and affect herd growth and that the

variables limiting herd growth are mortality or dispersal" (Bergerud 1971, 1980; vide Gauthier 1984:3). Movement and physical contact stimulate breeding activity. Therefore, sexual activity diminishes with reductions in mobility and animal density and is likely to result in decreased calf production (Bloomfield 1979). He added that range discontinuity and band isolation compound the problem. A final point, Bergerud et al. (1984:19) believed

> "that male and female caribou have far different parental investments because of polygynous breeding. The male's fitness depends on intrasexual competition for females. His role in propagation ceases upon breeding. The female must continue her care until the calf has a reasonable chance of survival or dies. Because of the investment differences females can be expected to be more wary and select more predator-free habitats than males, even at the expense of optimal foraging. Thus, disturbance reactions are greatest on the calving grounds after the birth of the calves."

Predation is the most important cause of death of calves in most herds. Herds exposed to predation usually lose 50 percent of their calves by 6 months of age (Bergerud 1978b). Other factors that may affect calf survivorship include: stillbirths, birth defects, exposure to weather, drownings, accidents and social interactions (i.e. trampling). Common causes of death for adults include: drowning, fighting between males, deaths in parturition, disease and/or parasites, accidents and predation. In general, herds without predators show population growth; whereas populations coexisting with predators show little or no growth and if also hunted usually show population decline (Bergerud 1980).

Little has been documented on the social behaviour of woodland caribou populations inhabiting closed forest. Simkin (1965), Shoesmith

(1978) and Darby (1979) all agreed that caribou were gregarious in winter and essentially solitary in summer. Evidence concerning the movements of woodland caribou in the boreal forest of Manitoba suggests that they do not undergo long migrations between summer and winter range, but rather, they undergo seasonal shifts of up to 64 km (Carbyn 1968; Crichton 1974; Darby 1978; Shoesmith 1978; and Stardom 1977).

Undisturbed lichen-plant communities and mature forests have been the traditionally accepted habitat requirements for woodland caribou. Recent findings suggest that this concept may not be universally true because these animals are very adaptable in their feeding strategies and possess catholic tastes. Compared to other ungulates, woodland caribou utilize a much wider variety of plant, animal and mineral material (Skoog 1968). Most green and flowering plants eaten by caribou have nutritionally satisfactory, if not high, protein contents; while, lichens have been judged to be protein and/or mineral deficient (Kelsall 1968). Ahti and Hepburn (1967) provided a thorough list of plants eaten by woodland caribou.

Bergerud (1972) studied the food habits of Newfoundland caribou and found that as the spring thaw advanced, the animals quickly changed their diet from lichens, mosses and liverworts to rapidly growing green plants. The most important of these green plants are grasses, sedges (Carex spp.) and cotton-grass (Eriophorum spp.). Catkins of willow (Salix spp.), leaves of birch (Betula spp.) and alder (Alnus spp.) and the buds of sweet gale (Myrica gale) were also important. In summer, reindeer moss (Cladonia spp.) is important, but caribou prefer the

green leaves of deciduous shrubs, especially willow, birch and blueberry (Vaccinium spp.). Caribou are fastidious feeders stripping the leaves from woody stems and picking only new sprouts and finer stem-tips of sedges, herbs (Hippuris spp.) and horsetail (Equisetum spp.). In late summer they actively search for fungi which have an exceptionally high protein content and are rich in fat and minerals (ash) (Kelsall 1968). Once deciduous forage dies with the first frosts of autumn, caribou switch to terrestrial lichens, broadleaf evergreens (Arctostaphylos) and sedges (Darby 1978). During winter, caribou are most often found in vegetationally suitable areas (Stardom 1975). The abundance of food and snow cover, operating singly or together, could be major factors either in increasing or decreasing the effect of thick snow in locating food (Edwards 1956). Since lichens have been judged to be protein and/or mineral deficient, then "winter-greens" such as labrador tea (Ledum groenlandicum), herbs, sedges and horsetail become important if caribou can locate them via cratering (Kelsall 1968, 1984). In addition, caribou seek the fragile twig ends of birch, willow and blueberry. If a sun crust develops on the snow that can support the animal, they will shift from open habitats to forest cover seeking arboreal lichens growing on coniferous trees (Bergerud 1978b) or shift to ground lichens on wind-swept ridges as a result of sun, surface or wind crusting (Stardom 1975).

HYPOTHESES FOR THE DECLINE OF WOODLAND CARIBOU

Several authors have proposed hypotheses to explain the historical decline "meaning fewer animals in a discrete population rather than the frequent shift of ranges in response to various

environmental factors which are normal" (Bergerud 1983:20) of caribou populations they studied. Bergerud (1974) after reviewing the literature developed arguments for two hypotheses: (I) numbers decreased because of a shortage of lichen supplies caused by fire and logging; and (II) populations declined because of increased hunting mortality, augmented by increased natural predation of some herds by wolves. Karns (1967) offered a third hypotheses that faunal changes caused by disturbed habitat can result in increased disease exposure for caribou, in particular meningeal worm (Parelaphostrongylus tenuis) transmitted from white-tailed deer.

Much has been written on the environmental impact of resource development in the tundra region to barren-ground caribou (Rangifer tarandus groenlandicus); but little has been written on the impact of logging to woodland caribou of the boreal forest. This imbalance can be explained by the relative unimportance placed on woodland caribou as a resource due their numbers. The following discussion will attempt to present material that directly correlates with the potential effects that logging has on woodland caribou and reindeer (Rangifer tarandus tarandus).

Hypothesis I: Food Limitation

Bergerud (1974:757) offered relevant premises in his discussion of this hypothesis: "(1) survival of caribou depends on the abundance of lichens (general rule); (2) settlement accelerated the frequency of forest fires and logging that destroyed climax lichen stands, which require many years to regenerate. This widespread destruction

coincided with the caribou decline following settlement (observed fact); and (3) hence man's impact in reducing the habitat and forage supplies caused the decline of the herds (inferred fact)."

It becomes apparent that if there is any credance to this hypothesis, a determination of the value of lichen (mostly Cladonia, Cetraria and Stereocaulon) to caribou winter ecology is imperative. Klein (1970; vide Schraeder 1982:6) proposed that

> "caribou enter a state, during winter, which has been referred to as physiological dormancy. Their growth levels off, food intake is reduced, metabolic rates drop, protein demand declines and carbohydrate catabolism sustains basal metabolic, locomotary and body heat requirements".

Since lichens are high (94%) in digestible carbohydrates which take the form of complex starches, Klein (1982) proposed that lichens should therefore be a good source of energy. Nieminen et al. (1977) claimed that the nutritional value of lichens is to provide a source of readily digestible carbohydrate that has a synergistic effect in increasing the digestibility of cellulose and hemicellulose. In contrast, Bergerud (1974) after reviewing Courtright (1959) and Kelsall (1968) suggested that caribou would be unable to maintain their body weight if fed an ad libitum diet of only lichens (due to their low protein content). Some authors believed that caribou do not require lichens in winter and, in many instances, feed primarily on other foods. Skoog (1968) indicated that caribou in Alaska extended beyond their normal range boundaries even though good lichen stands were available nearby. The presence of ground lichens by themselves does not prove that caribou will selectively choose to winter in these areas (Cringan 1957; Stardom 1975).

According to the food hypothesis, forage availability (particularily of lichens) in winter, as influenced by snow characteristics, is considered the principal limiting factor to caribou herd growth; while during summer, if ranges utilized by caribou are disturbed, there is a potential for a decrease in feeding time or an increase in energy demands, especially preceeding or following a winter of thick snow (Gauthier 1984). Regardless of the situation, winter survival is dependent on an animal's capability of drawing from its fat reserves built up during the summer period of vegetative growth (Klein 1982).

> "If food supplies are limiting herd growth, it follows that the rate of increase of the herd should show some decline as numbers increase and no such relationship has been documented" (Gauthier 1984:7).

Bergerud (1983) was only able to find 2 examples of free-ranging caribou inhabitating the boreal forest where mortality resulted from starvation. In addition, neither the reproductive rate nor the mortality rate of free-ranging caribou have been affected by a reduction in absolute abundance of forage (Bergerud 1974). Although, Dauphiné (1976) believed that a poor dietary regime as influenced by the character of snow cover would decrease recruitment through poor prenatal nutrition by initiating fetal resorption, the production of calves of low viability or the failure of a cow to breed.

Lichen Biology

Lichens represent a symbiotic relationship between fungi and algae which are morphologically and physiologically different from either organism as it exists separately. Fungi which are the dominant

partner, hold the algae captive and are dependant on the algal cells for nourishment. Lichens are frequently very desiccated in nature, with a water content ranging from 2 to 10 percent of their dry weight. As lichens dry out photosynthesis ceases, and in this state of suspended animation blazing sunlight or great extremes of heat or cold can be endured. When a lichen is moistened by rain, it absorbs 3 to 35 times its own weight in water in a very short time. Lichens reach their maximum vitality, as judged by the rate of photosynthesis, after being soaked with water and drying begins. The rate of photosynthesis reaches a peak when the water content is 65 to 90 percent of the maximum it can hold; if lichens lose water, the rate of photosynthesis decreases. In many environments, the water content of the thallus (plants not clearly differentiated into root, stem and leaf) varies markedly in the course of the day. Most photosynthesis takes place in the early morning after wetting by fog or dew. As a consequence, lichens are geared to an extremely low rate of growth. Lichens apparently absorb some minerals from their substrate (this is suggested by the fact that particular species are characteristically found on particular kinds of rocks or soils or tree trunks), but most of the elements absorbed by lichens enter the plant from the air and in rainfall. These elements are absorbed rapidly and are concentrated within the lichens' thalli. Because lichens have no means of excreting these elements, lichens are susceptible and sensitive to toxic compounds and lichen growth is a sensitive indicator of polluted air (Raven and Curtis 1971).

Environmental Impact of Logging on Lichen Growth

Reindeer moss (Cladonia spp.) that caribou most often utilize require high relative humidities, a thin humus or mineral soil layer for attachment and vast amounts of sunlight (Ahti and Hepburn 1967). Klein (1971) claimed that reindeer herders complain that logging activities damage the lichens on the forest floor and that changes in the microclimate, caused by the removal of the forest cover, reduce the growth rate of lichens. Because the wind causes snow within large clear-cuttings to drift and compact, it is generally more difficult for reindeer to feed in these areas than in the undisturbed forest. In support of this, Eriksson (1975:112) stated that

> "studies where changes in climate after logging have been recorded were published by Odin and Perttu (1966), Odin (1971) and Perttu (1973). Some of the results from their studies on clearcut areas and in adjacent, somewhat scattered forest close to the treeline in the county of Norrbotten Sweden (probably the most intensively utilized area by the reindeer industry), may be synthesized as follows:
>
> a) No obvious difference in temperature at standard level (200 cm) between a clearcut area and the surrounding forest.
>
> b) Close to the ground (less than 50 cm) the clearcut area was warmer in daytime and colder at night than the surrounding forest.
>
> c) The number of night frosts during summer was greater in the clearcut area than in the forest.
>
> d) Surface temperature in the clearcut area was about 15°C higher than in the surrounding forest on a hot summer's day.
>
> e) The capacity for evaporation from the ground vegetation was about 40 percent higher in the clearcut area than in the forest.

f) Wind speed in the clearcut area was 80 percent higher than in the surrounding forest.

g) Net insolation during a cloudless summer's day was 50 percent higher in the logged area than in the forest.

h) Snow cover thickness in the clearcut area varied greatly due to exposure to wind."

Insolation levels that are too high or too low will restrict lichen growth as will drought. Hence, a clearcut area is a poor environment for lichens since insolation is unrestricted and humidity is lower than in a forest (Eriksson 1975).

Aside from the direct environmental impact that logging operations have on lichen growth, additional complications arise. Vehicular traffic, during and after a timber extraction operation, driving on the fragile mats could result in the scraping off of lichen or cause a compression of the lichen mat. This most certainly would kill or displace plants, possibly more so, if dry or frozen.

A point of interest, Klein (1971) claimed that herbicides used in forestry were implicated in the death of several reindeer in Sweden in 1970. During a period when thick snow cover made lichens unavailable, reindeer fed on leaves from birch trees that had been killed by herbicides (2,4-D and 2,4,5-T).

Caribou Behaviour in Relation to Logging

Caribou can be nomadic and migratory with survival contingent upon the maintenance of suitable travel corridors interconnecting areas of special significance (i.e. rutting, calving and wintering grounds)

(Bloomfield 1979). Due to large groupings of caribou, there is potential for large scale detrimental impact caused by resource development. Mahoney (1980) felt that the response to leadership may be responsible for very large groups following the actions of one or a very few animals. Thus, where caribou encounter a disturbance, the reaction of a single group leader may result in several hundred animals adopting the same response (perhaps this is what happened in Quebec 1984). Bergerud (1985 pers. comm.) on the other hand, believes that there are no leadership tendencies in caribou -- first animal then the next. Miller et al. (1972) claimed that the ultimate consequence of range discontinuity is the isolation and over-exploitation of individual bands, reductions in intergroup contact and an increase in the chance of forage over-utilization, predation and social disorganization. Adjustments in route alignments could destroy herd traditions (based on environmental cues) and cause increased vulnerability by forcing caribou into unfamilar areas. Since lichen regeneration rates are slow, changes in range become vital to caribou survival as it prevents over utilization of the range. Therefore, it is important that caribou have a proportionately large and flexible home range (Edmonds 1983 pers. comm.).

Eriksson (1975) wrote that during winter, an occasional spell of mild weather may cause a thin snow layer to thaw to ground level. With the return of cold weather, the wet snow on the ground will freeze to an icy crust making grazing more or less impossible. There is a greater risk of getting hard snow cover in an open area than in forests

(Rodhe 1965). Layers of icy snow or tough compressed snow also tend to develop more often on open ground than in forests (Rodhe 1965; Eriksson, 1972). Snowcover can limit food supply (Darby 1979). Stardom (1975) found that woodland caribou tended to avoid areas of snow where the thickness surpassed a threshold of 65 cm.. This occurs first in bogs (and could develop in large cutovers in addition to drifting or sun crust development) and consequently caribou would need to use the forested ridges where the snow cover is softer and not as thick. Bergerud (1978a) stated that

> "given an equal opportunity to choose between arboreal and terrestrial lichens, animals will take terrestrial ones since more effort is involved moving between trees than feeding on a continuous cryptogamiam mat (plants such as algae, mosses and ferns which do not bear true flowers but grow from spores)."

However, at some point digging craters will require more energy than moving between trees. Bergerud and Nolan (1970; vide Gauthier 1984:98) concluded that

> "caribou cannot detect the presence of lichens through snow cover greater than 25 cm thick unless holes are present such as those made by plant stems."

The law-of-least-effort maximizes reproductive fitness by minimizing expenditure on maintenance activities and thereby saving it for reproduction.

Gauthier (1984:97) believed that

> "the interaction of forage and climatic conditions, particularly snow thickness and hardness in winter, windchill and precipitation conditions during calving, influence caribou mortality rates in three important ways: (1) restriction of access to forage in winter due to snow thickness and/or hardness with resultant increases in starvation rates and/or increases in vulnerability of individuals to other mortality factors;

> (2) increasing susceptibility to predators due to differential mobility of caribou and predators under differing conditions of snow thickness and hardness; and (3) large-scale mortality due to direct influences of weather and death of neonates due to inability to withstand severe combinations of wind, temperature and precipitation (Kelsall 1968)."

Caribou select different habitats during the year in response to seasonal forage preferences (Mahoney 1980) and as a predator avoidance strategy (Roby 1978). Klein (1970; vide Mahoney 1980:5) pointed out that

> "during the summer, nutritional requirements for growth, fattening and lactation are high and caribou select the highest quality forage available".

Klein (1980) also felt that adding disturbance through other human activities will nevertheless lead to increased physiological costs to the animals. These costs may be met through increased forage intake (if this option is available), altered behavioural patterns (accommodation to the disturbance or abandonment of areas of disturbances), or reduced allocation of energy to other requirements (growth, reproduction and escape from predators). Mahoney (1980:6) further stated that

> "distribution patterns of caribou are influenced by other factors besides forage and predation. Physiological influences and in particular endocrine levels during parturition and rut, have important roles to play in regulating caribou activity and movement, rumen capacity and turn-over rate, nutritional deficiencies, insects, disease and injuries all work to affect caribou distribution. These factors usually dictate the reaction of caribou to any disturbance. Furthermore, these influences perform interdependently, and subtle changes in any one parameter may be responsible for a pronounced cumulative response."

What then is the consequence of temporary disruption of traditional movement patterns, due to environmental cues, of caribou or reindeer? Espmark (1970) felt that domestic reindeer movements are based on learned familiarity with topography, vegetation and snow conditions along a route. If traditional routes are severely altered, a herd's social organization could be destroyed and the herd could become disorientated, especially young animals. Pregnant cows, both reindeer and caribou, tend to return to the vicinity where they gave birth the previous year. Yearlings and young females pregnant for the first time tend to follow the older, experienced females thus maintaining the traditional use of a specific area for calving. If movements to the calving grounds are delayed or stopped so that calving occurs in a new area, presumably females calving for the first time will tend to move to the new area in subsequent years and older females will experience a weakened homing drive to the traditional calving grounds. Klein (1980) noted that there is some evidence from North America that when caribou herds are at low levels, their traditional patterns are more tenuous and therefore more subject to disruption than when population numbers are at or near the long term mean.

Mahoney (1980:6) thought

> "that preventing parturient cows from reaching their traditional calving grounds or disturbance in these areas could have a potentially disastrous impact on survival of young. On their extensive ranges caribou select only restricted areas for parturition; these calving grounds are the most predictable elements of caribou ecology and provide these animals with the specific conditions essential to successful reproduction. The disruption of calving could affect recruitment as might displacement of parturient cows and/or neonates from feeding or resting activity. The latter, however, is much more difficult to quantify."

Klein (1980:525) concurred by stating that

> "if traditional calving areas are lost the consequences may be lowered calf survival through use of less favorable calving areas (i.e. increased threats to calf survival from unfavourable weather, increased predation, insect harassment and greater presence of other natural or man caused hazards as well as shortage of good quality forage). Loss of access to insect relief areas may reduce feeding opportunity, lead to increased energetic expenditure, reduce growth rates of young and curtail the deposition of body reserves in preparation for breeding and winter".

Hypothesis II: Increased Predation and Human Harvest

Woodland caribou have evolved to utilize secluded mature and semi-mature habitat where moose and deer are absent or rare. The disturbance of these forests (clearing of land for agriculture, timber extraction, road and rail development, hydro development, fires) results in depreciated caribou habitat and range. This alteration from old forests to young successional forests permits the invasion and increase of moose and deer. As the relative abundance of cervids increases, the profusion of predators (bears, wolves, wolverines, lynx, foxes, eagles), hunting by man and disease also increase (Kelsall 1984).

Predator-prey Theory

To understand the predatory impact on a population, one must first become acquainted with a predator-prey theory. Refer to May (1976), Poole (1974) and Maynard Smith (1974) for general references

dealing with predator-prey models. For the purpose of discussing this hypothesis, the following two presentations of the predator-prey theory were chosen because they were used to address the predator-caribou relationship.

Heard and Boutin (1982) presented their theory that logistic population-growth can be represented by a dome-shaped net reproduction curve. Net reproduction expressed as a percent of population size declines linearly with increasing population size and is determined by the combined impact of birth and death rates. Because caribou birth rates vary little, the percent net reproduction curve can be considered to be solely a function of changes in mortality.

Holling (1959; vide Heard and Boutin 1982:2) demonstrated that

> "predators can respond to changing prey densities in two ways: functionally and numerically. Functional responses refer to the ability of predators to capture and consume their prey at different prey densities. The numerical response refers to the predator's ability to convert prey into more predators. The functional response curve shows saturation at high prey densities because predators have a minimum handling time per prey. The numerical response curve also asymptotes because, like all populations, predators cannot continue to increase indefinitely."

Holling (1959; vide Heard and Boutin 1982:6) further stated that

> "functional and numerical response curves are linked to produce a combined predation mortality response curve indicating the proportion of prey eaten at varying prey densities. At low prey densities, predators take a greater proportion of prey as prey numbers increase. Beyond a certain density the proportion taken decreases with increasing prey density because of the saturation behaviour of the functional numerical response curves. The key point is that if predation is high enough to regulate prey numbers it may do so only over a restricted range of relatively low prey densities. Once prey numbers move beyond that range, predators have less influence on prey population sizes."

Bergerud (1985 pers. comm.) believes the opposite to be true--caribou escape predation at low densities.

Theberge and Gauthier (1985:449) proposed 7 descriptive models based on an analogy that provided a framework within which to consider the complexity of wolf-ungulate relationships, together with supporting evidence for each model. They considered

> "an ungulate population as a buoy fully submerged in water. Population size is depicted by the height of the buoy in from the bottom. The surface of the water represents a carrying capacity set by nutrition quality/quantity modified by climate and is the upper level of potential population size. Attached to the buoy by a strong elastic cord is a submerged weight, which is not on the bottom but in dynamic equilibrium with the buoy. The height of the weight from the bottom represents the size of the predator population. The size of the ungulate population (height above bottom of the buoy in the water) is a function of the carrying capacity (height of the surface of the water) and the predator effect (height of the weight). One can think of the predator/prey ratio as the relative heights of the weight and buoy, and any change in the distance between the two is a reflection of the degree of influence of the predator on the prey. The predator effect is a function of the size of the predator population as well as predator efficiency, food preferences, and prey vulnerability. Thus, the connection between the buoy and weight is elastic, allowing the distance between the two to vary under different conditions. The elastic connection does not provide any push-pull relationship in the analogy, but only provides the opportunity for the distances to vary."

Gauthier (1984:12) used the following assumptions to test the predation hypothesis:

> "(1) that predation is the major mortality factor; (2) that the effects of predation on herd numbers are additive, not compensatory, relative to other mortality factors; and (3) that predation acts to significantly reduce prey numbers below other threshold levels of limitation."

Gauthier's review of the factors most likely to be limiting caribou numbers suggests the following

> "predictions should be upheld if the predation hypothesis (as an explaination of changes in numbers) is correct: (1) productivity should not vary significantly among years, (therefore, pregnancy rates should remain relatively stable); (2) assessment of animal physical condition should indicate that animals are healthy, relative to known baseline indices; (3) habitat analyses should show relatively abundant and available seasonal forage; (4) indices of climate severity during winter and calving periods should not be related to mortality rates; (5) studies of predator food habits should show that the number of caribou eaten by predators is significant in relation to caribou productivity, i.e. predators are the major mortality factor."

Gauthier (1984:13) further stated that

> "in a complex system of changing, interconnected casual factors, probability estimates are our best means of attempting to apportion the degree of casuality. Note that none of the predictions by themselves, if upheld, is sufficient to show that predation is the major limiting factor to caribou herd growth. However, rejection of prediction 5 would provide grounds to reject the hypothesis, whereas rejection of predictions 1,2,3 and 4 would at least confound conclusions that could be made regarding the role of predators in limiting herd sizes."

Wolf-caribou Association

Disturbance of caribou habitat and range can also potentially affect caribou indirectly, through alteration of predator-prey systems. Bergerud et al. (1984) believed that the major environmental variable that permits caribou to co-exist with predators is space. Caribou need extensive areas so as to space themselves far from denning wolves. Again, space is needed that will provide habitats where caribou have an advantage such as mobility. The greater the space the greater the

dispersal of caribou, thus the greater the searching time for wolves. Since the reproductive rate of caribou is low and the mortality rate among calves is exceedlingly high (Kelsall 1968; Bergerud 1971), an increased abundance of wolves could be sufficient to initiate a decline in the herd. Therefore in the author's view, if this space is reduced due to the alteration of habitat, it is conceivable that predation rates could increase due to the increase in other prey species (mice, moose, deer) which in turn could increase predator numbers thus increasing predator-caribou contact (by associated wolf movement). Subsequent declines could result when the increased prey species decline leaving the wolf population stranded forcing it to switch to caribou.

> "Wolf numbers are rated as normal if the wolf population is about one wolf per 65-130 km^2 with caribou and moose the primary big game prey, or one wolf per 260-390 km^2 if only caribou are the main prey. Caribou densities are considered normal if densities approximate 0.4 animal per km^2 and low if densities are 0.2 animal per km^2 " (Bergerud 1983:27).

There are numerous examples where populations of caribou, which co-inhabit the same areas as moose and/or deer (Lake Nipigon Islands, Ontario; Pukaswa National Park, Ontario; Reed Lake, Manitoba; Sasaginnigak Lake, Manitoba; Wallace-Aikens Lakes, Manitoba) appear to make extensive use of large insular complexes in large lakes throughout the summer. Even though many of these complexes are unattractive in terms of abundance or quality of food, it is postulated that cows move to islands to avoid wolves and insect harassment during calving (Bergerud and Butler 1975; Cumming 1975; Shoesmith 1978; Darby 1979).

Crichton (1985 pers. comm.) on the other hand does not believe that islands provide much relief from insect harassment since insects are found on islands as well. He also believes that islands do not provide anti-predator refuges but rather offer a fast get away (to water) to escape predatory pursuits. In winter, when ice forms access bridges, the summer island refuges cease to be anti-predator effective. Perhaps the caribou form anti-predator wintering aggregations but locate them in areas where food is abundant (Cumming and Beange,in press) or where they can see well (Cumming 1975).

Human Harvest

Kelsall (1984) cited Banfield (1954), Bergerud (1974 and 1978a), Fuller and Keith (1981) and Bloomfield and Sword (1981) as but a few of the authors who have suggested that hunting by itself or in combination with other factors has either extirpated, reduced or may now threaten woodland caribou populations. Caribou are more susceptible to over-harvest than any other North American cervid particularly because of their lack of aversion to man, traditional habits (wintering areas vs calving areas) learned behaviour (a tendency to make and follow their own trails often crossing roads at fairly well defined locations), their apparent non-recognition of stationary objects, gregariousness and low recruitment rates (Bloomfield 1979). Any significant increase in mortality unaccompanied by offsetting gains would upset the delicate balance between mortality and recruitment and cause a population decline. In addition, when predators are left undisturbed, there really are no surplus woodland caribou available for human harvest.

Mahoney (1983 pers. comm.) emphasized that the most conspicuous and damaging of all impacts from human disturbances is increased access; not to mention, the use of new and improved technology in hunting, such as high-powered rifles, all-terrain vehicles, snowmobiles, aircraft and night lights all contribute to increased hunter efficiency. Once a road or line is provided, preventing access is all but impossible particularly in winter time when snowmobile travel is much facilitated by the obstruction-free surface. This, via both legal (licenced and Treaty harvests) and illegal hunting (even by inexperienced people), will certainly affect caribou numbers and distribution, particularly where such access is provided to the periphery of previously undisturbed habitats and population ranges.

Woodland caribou could be listed as an endangered species in the Manitoba Wildlife Act for specific game hunting areas where mortality due to subsistence hunting is additive. This would minimize the potentially disasterous impact of increased access and further prevent extirpation of caribou populations. However, this course of action would be charting new waters since no case law exists to demonstrate its potential effectiveness in protecting a species.

Hypothesis III: Parasitic Infection Due to Faunal Changes

Recent research has introduced a new concept into the controversy of why woodland caribou declined in eastern North America. Evidence suggests that the coincidental invasion of caribou range by white-tailed deer eventually led to additional caribou mortality through neurological disease caused by the meningeal nematode (Parelaphostrongylus tenuis).

Anderson (1972) writes that the white-tailed deer is a highly adaptable animal most typical of the deciduous forest biome. Its northern range has expanded remarkably during the past century largely

as a result of human activities (fire, forestry and agriculture) which have in many regions broken up the mature deciduous-coniferous forest and the adjacent coniferous forest. This northern range of expansion has brought the host (white-tailed deer) and the parasite (meningeal nematode commonly found in deer in many areas) into contact with other native cervids such as moose, woodland caribou, elk and mule deer. In these animals the parasite is highly pathogenic. There are no reports of meningeal worm in the grassland biome of central North America (Bindernagel and Anderson 1972). Prior to settlement, the climax deciduous-coniferous forest in northern Minnesota and southern Manitoba may have acted as a barrier to the spread of the parasite from the deciduous forest biome into the aspen parklands. P. tenuis has been found in white-tailed deer in the aspen parklands of Manitoba and eastern Saskatchewan (Bindernagel and Anderson 1972). Although the grasslands might act as a barrier to the westward spread of the parasite, the aspen parklands could serve as a corridor by which the parasite could reach western North America. A note of interest, in Newfoundland (historic record goes back over four centuries) white-tailed deer and P. tenuis have not reached the island, and the caribou are thriving (Kelsall 1984). Another parasite, Elaphostrongylus cervi, has been reported in caribou of Newfoundland (Lankester and Northcott 1979) and spiny tailed larvae similar to those of E. cervi and P. tenuis have been reported in caribou of Manitoba and Ontario (Lankester et. al. 1976). This parasite is a well known agent of neurological disease in reindeer of Eurasia.

The status of knowledge regarding the significance of the meningeal worm to woodland caribou is limited to experimental studies (Trainer 1973). In the past, since there is no evidence in the

literature of neurologic disease in caribou, such a disease syndrome might have been overlooked, unrecognized or unreported (Anderson and Strelive 1968). The parasite probably should be recognized as a potential factor in limiting population increases where woodland caribou range is associated with white-tailed deer. The only viable caribou population now coinhabiting range with high densities of deer is on the Shickshock Mountains, Gaspé, Québec (Bergerud 1978b). Vertical stratification (caribou high, deer lower down) may be the means that contact is minimized.

Evidence on which to attribute the disappearance of caribou to neurologic disease is largely circumstantial. The disease hypothesis can be confirmed only by recovery of adult P. tenuis in fresh or otherwise well-preserved caribou specimens (Dauphiné 1975). But introduction failures of woodland caribou onto range now occupied by white-tailed deer with a prevalence of meningeal worm (as predicted by Anderson and Strelive 1968) in Cape Breton, Maine, Minnesota, Ontario and Wisconsin support this hypothesis.

TWO PROVINCIAL CUTTING PROPOSALS

Most timber harvesting operations in the boreal forest employ the clear cutting method to remove merchantable timber. Since most stands in the boreal forest are of fire origin, and thus nearly even aged, logging leaves few trees except where non-merchantable patches occur (Telfer 1974). Logging therefore acts like fire to cause reversion of extensive areas to young stands, often composed of plant communities

characteristic of stages of secondary succession. Unlike fire, logging does not typically destroy the humus layer but in both cases, the subsequent regeneration of vascular plants could inhibit Cladonia spp. production resulting in a long term (in respect to caribou; approx. 80-150 years in northern Manitoba) loss of winter forage. In the short run though, Salo (1975) believed that logging could result in an abundance of arboreal lichens since caribou could graze on lichens present on felled trees. Since range balance is important to wildlife, the impact of logging depends on the adopted pattern. Therefore, size and shape of cut areas, and uncut residual stands, location of cut and uncut areas on the topography, and species composition of uncut stands will all affect range balance (Telfer 1974). This may ensure timber reserves within cutovers from becoming isolated islands of suitable habitat that caribou avoid (Brousseau 1979).

To achieve compromise in minimizing habitat disturbance for woodland caribou, Alberta (Edmonds and Bloomfield 1984) and Ontario (Duquette 1984 pers. comm.) have taken similar and yet contrasting approaches to timber harvesting guidelines. These appear to be based on regional differences in forest extraction practices within regional differences in caribou habitat. These guidelines are as follows:

ALBERTA

Cut Plan a) wet organic soils (leave blocks vulnerable to blow down)

- conventional cutblock configuration
- minimizing edge

- a 3 pass system with cuts to be 50 years apart so that one third of the forest is maintained at a minimum of 100 years of age.

b) good terrestrial lichen forest habitat

- cutblock configuration can be large in area (300 ha)
- cutblocks should be narrow strip blocks with a width no greater than 150 m.
- a 3 pass system with cuts to be 25-30 years apart to provide adequate time for terrestrial lichen regeneration.

c) non-suitable forest habitat

- conventional square cutblocks designed so that there will be no barrier to movement by caribou, ie. adequate forest cover (≥3.6m stand height) is available in a continuous distribution through the area
- a 2 pass system.

Logging - on primary use areas should take place in summer

- to be ceased during calving or breeding seasons within areas known for these activities
- if necessary during winter, on primary use areas (ie. due to wet soils or a need for continuous wood supply) should be concentrated in one portion of the winter range rather than distributing the activity (disturbance) throughout the winter range.

Roads - should not be situated on ridge tops or through meadows (except to facilitate crossings)

- amount of long term "ATV usable" spur roads must be kept to a minimum
- all spur roads will be naturalized as soon as possible after logging

Site Treatment - terrestrial lichen habitat will not be scarified, although some experimental blocks will be lightly scarified.

ONTARIO

Cut Plan -large clear-cuts (130ha.- 500 ha.) versus numerous small clear-cuts (equalling 130ha.)

Several small clear-cuts result in more widely dispersed habitat disturbance, greater road access of longer duration and, frequently, higher moose and deer densities than a single large cut.

Logging - may be acceptable in portions of winter range other than sensitive habitats if caribou winter use is infrequent or if lichen biomass is low.

- should not be allowed within 2 km of the core of prime winter range
- should not occur within sensitive habitats (calving and wintering area)
- should not be allowed within 1km of shorelines adjacent to known calving islands

- other silvicultural methods (shelterwood, selective cutting) have been assessed and discarded as inappropriate

Roads - where possible, should be scarified

- access to recent cutovers may be discouraged with user controls such as signs and gates

Site Treatment - where sub-optimal portions of the winter range are cut, regeneration of lichen stands within the cuts is an important management objective. The following procedures are recommended:

i) recent cut-overs should be lightly scarified (Eriksson 1975);

ii) prescribed burn treatment is not recommended because the nutrient flush following burning may favor an influx of vascular plants and feather mosses onto the site;

iii) slash remaining from cutting operations should be left scattered over the site to provide substrate for lichen colonization and to increase humidity close to the ground (Eriksson 1975);

iv) lichens should be seeded onto the regeneration area once the site has been prepared (Bergerud and Butler 1975);

v) the use of chemical sprays to reduce deciduous regeneration may be warranted. However, chemical sprays should be used with caution as lichens may also be adversely affected by their use.

Stevenson (1985 pers. comm.) suggested if arboreal lichen production is to be a primary concern, then selective cutting could be considered as an experimental management alternative. Typically in a closed canopy, lichens are distributed according to light penetration areas. If light is considered to be the limiting factor to lichen growth, then the canopy can be opened by selectively removing trees. Although there would be an initial decrease of approximately three-quarters of the existing lichen biomass, there is a potential for enhancing lichen growth (Stevenson 1979). The opportunities for lichen fragments to disperse onto young trees and begin growing are much improved by the presence of residual, lichen-bearing trees; whereas, clearcutting removes all lichen. A selectively logged block is expected to regain its former level of lichen biomass in less time than a clearcut block. A word of caution, a selectively logged stand will increase road access and furthermore, Hammond (1978) estimated that 23% of the area would be converted into a clearcut by the construction of landings, skid roads and haul roads.

RECOMMENDATIONS

Lichen survival is assured by a symbiotic relationship between fungi and algae and it is essential that a similar type of relationship exist between foresters and wildlife biologists to ensure preservation of the myriad of wildlife species. It is inevitable that resource development will invade caribou range and this review shows the potential negative impact that logging has on woodland caribou

populations previously isolated from human activities. We must therefore co-operatively protect critical areas vital to herd welfare while negotiating the management of remaining areas to lessen the impact of logging. In light of Manitoba's sparse caribou herds and thus their fragility, the following is recommended:

A) Identification of critical woodland caribou habitat (wintering areas, calving areas, rutting grounds and migration routes) is to be determined by Wildlife Branch before development activities begin. (Refer to Storey and Storey 1980 for woodland caribou habitat evaluation as a possible assessment technique, review historical use patterns or interpret Landsat imagery);

B) Develop management guidelines for development areas which are specific to individual caribou herds. The following recommendations are put forth with the suggestion that they be followed until tested and/or refined guidelines for specific herds are formulated:

   i) detailed cutting plans are to be submitted to Wildlife Branch at least 2 to 3 years in advance so that the Branch may determine the impact of such activities and give direction to harvesting companies so that the impact is minimized;

   ii) thoughtful consideration to the placement of roads within caribou habitat to be given prior to construction and the Wildlife Branch is to be involved in the initial planning and discussion phase;

iii) critical habitat (i.e. traditional wintering, calving and rutting areas) are to be designated as Wildlife Management Refuges thus giving management authority to the Wildlife Branch. A buffer of at least 2km to be retained around the outermost perimeter of these areas;

iv) avoid conflicts between logging operations and caribou migration by retaining no less than 2 km of uncut timber along the migration route to provide necessary security (Porter 1983);

v) protect Manitoba's lightly to moderately stocked tamarack and/or tamarack/black spruce bogs from logging (Pruitt 1985 pers. comm.);

vi) protect lichen stands from vehicular traffic of any kind (Ahti and Hepburn 1967);

vii) where cutting is to occur, the lichen-rich rock ridges be avoided i.e. all activities restricted to lowland areas;

viii) where cutting occurs in caribou areas, these activities to occur in as short a time period as possible to avoid prolonged annual disturbances;

ix) close all forestry roads for a 2 to 4 week period to prevent disruptions to migrating animals (Porter 1983) and to restrict hunter access;

x) access roads adjacent to known caribou range or that enter into caribou range are to be rejuvenated in such a way that

access is restricted and the land base is put back into production where feasible;

xi) consider selective cutting as an experimental management alternative where arboreal lichen production is a primary concern (Stevenson 1985 pers. comm.);

xii) where cutting is to occur, a commitment be given by the Department of Natural Resources to document pre and post cut activity in the 'affected area' as well as formulating a long term program to document the 'rejuvenation' of caribou habitat in the said area.

C) List woodland caribou as an endangered species (under Section 7 of Manitoba's Wildlife Act) in Game Hunting Areas 14, 15, 15A, 17A and 26 to reduce additional mortality (Appendix II).

D) Reduce predator populations in key caribou areas if they are proven to be depressing the recovery of a caribou herd and if high predator populations are not required for other purposes at that particular location (Kelsall 1984). Managers have to decide what they want - " undisturbed predator-prey systems or huntable populations with reduced predator densities" (Bergerud 1983).

E) Prohibit cottage development and other recreational activities on islands critical to caribou during the summer (Cumming and Beange in press).

F) Limit the use of herbicides as silvicultural treatments of cut and uncut forests which caribou use since lichens are susceptible to toxic compounds.

G) Foresters and wildlife biologists to test the above recommendations in an experimental management area as well as address the disease potential.

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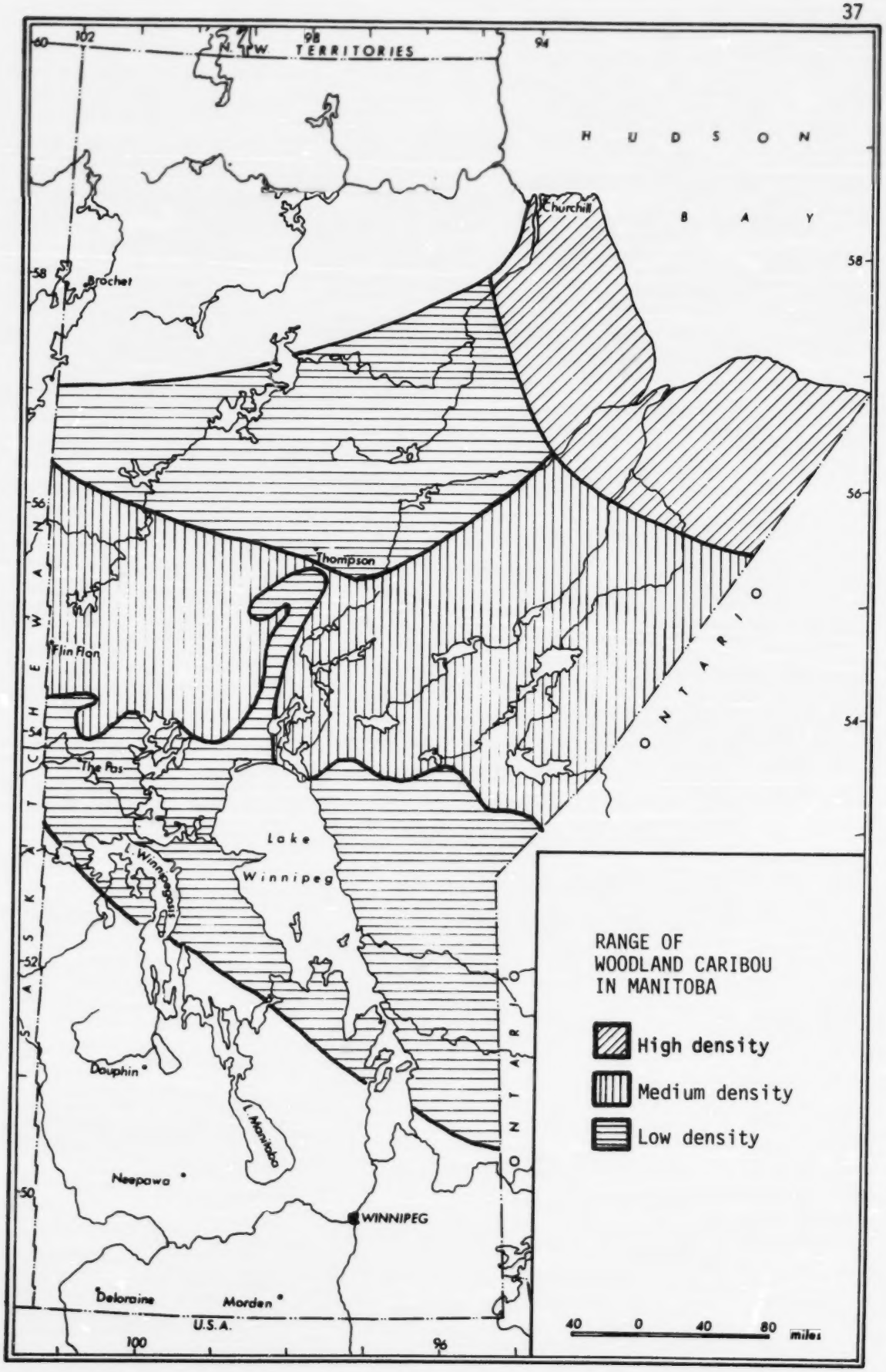
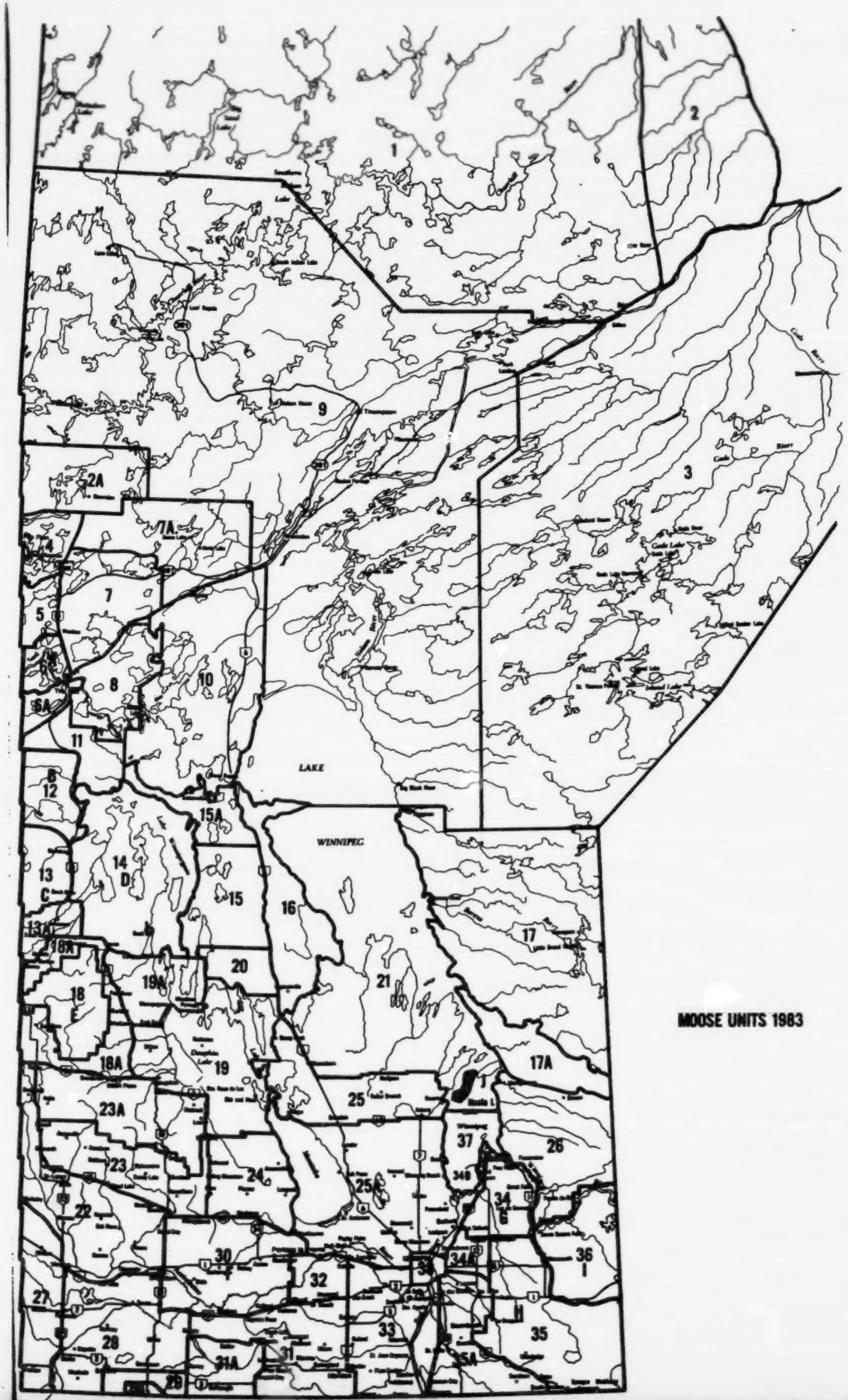
APPENDIX 1


N.W.T.
TERRITORIES
HUDSON
BAY
Churchill
Brochet
Thompson
Flin Flon
The Pas
Lake
Winnipeg
L. Winnipegosis
L. Manitoba
Dauphin
Neepawa
WINNIPEG
Deloraine
Morden
U.S.A.
SASKATCHEWAN
ONTARIO
RANGE OF
WOODLAND CARIBOU
IN MANITOBA
High density
Medium density
Low density
40 0 40 80 miles

APPENDIX II



MOOSE UNITS 1983

BIBLIOGRAPHY

Ahti. T. and R.L. Hepburn. 1967. Preliminary studies on woodland caribou range, especially on lichen stands, in Ontario. Ontario Department of Lands and Forests, Research Report (Wildlife), No. 74, 134pp.

Anderson, R.C.. 1972. The ecological relationships of meningeal worm and native cervids in North America. Journal of Wildlife Diseases, 8: 304-310.

Anderson, R.C. and U.R. Strelive. 1968. The experimental transmission of Pneumostrongylus tenuis to caribou (Rangifer tarandus terraenovae). Canadian Journal of Zoology, 46: 503-510.

Banfield, A.W.F.. 1954. Preliminary investigation of the barren ground caribou. Part II. Life history, ecology, and utilization. Canadian Wildlife Service, Wildlife Management Bulletin, Series 1, 10B, 112pp..

Bergerud, A.T.. 1971. The population dynamics of Newfoundland caribou. Wildlife Monographs, No. 25, 55pp..

Bergerud, A.T.. 1972. Food habits of Newfoundland caribou. Journal of Wildlife Management, 36: 913-923.

Bergerud, A.T.. 1974. Decline of caribou in North America following settlement. Journal of Wildlife Management, 38(4): 757-770.

Bergerud, A.T.. 1978a. The status and management of caribou in British Columbia. Province of British Columbia, Fish and Wildlife Branch Report, 145 pp.

Bergerud, A.T.. 1978b. Caribou. pp. 83-102 in J.L. Schmidt and D.L. Gilbert (editors). Big Game of North America. Ecology and Management. Stackpole Co., Harrisburg. 494 pp.

Bergerud, A.T.. 1980. A review of the population dynamics of caribou and wild reindeer in North America. pp 556-623 in E. Reimers, E. Gaase and S. Skjenneberg (editors). Proceedings of Second International Reindeer and Caribou Symposium. Roros, Norway. 799 pp..

Bergerud, A.T.. 1983. The natural population control of caribou. pp 14-61 in F. Bunnel, D. Eastman and J. Peek (editors). Symposium on Natural Regulation of Wildlife Populations. Vancouver, British Columbia.

Bergerud, A.T. and M.J. Nolan. 1970. Food habits of hand-reared caribou Rangifer tarandus L. in Newfoundland. Oikos 21: 348-350.

Bergerud, A.T. and H.E. Butler. 1975. Some rambling thoughts on caribou distribution and abundance in the Armstrong- Nipigon Region. Unpublished University of Victoria Report. 50 pp..

Bergerud, A.T., R.D. Jakimchuk, and D.R. Carruthers. 1984. The buffalo of the north: caribou (Rangifer tarandus) and human developments. Arctic, 37(1): 7-22.

Bindernagel, J.A. and R.C. Anderson. 1972. Distribution of meningeal worm (Pneumostrongylus tenuis) in white-tailed deer in Canada. Journal of Wildlife Management, 36: 1350-1353.

Bloomfield, M. 1979. The impact of development, settlement and associated activities on mountain caribou in central British Columbia, Canada. pp. 699-715 in E. Reimers, E. Gaare and S. Skjenneberg (editors). Proceedings of Second International Reindeer and Caribou Symposium. Roros, Norway. 799 pp..

Bloomfield, M. and M. Sword. 1981. Report to COSEWIC on the status of caribou populations in Alberta. Unpublished Alberta Fish and Wildlife Division Report, Edson. 63 pp..

Brousseau, C.. 1979. Trends in the woodland caribou (Rangifer tarandus) population in the Cliff Lake area of the Dryden district, 1972-1978. Unpublished Ontario Ministry of Natural Resources Report. 25 pp..

Carbyn, L.N. 1968. Woodland caribou survey in the Bloodvein River region of eastern Manitoba. Unpublished Manitoba Department of Mines and Natural Resources Report. 4 pp..

Courtright, A.M. 1959. Range management and the genus Rangifer: a review of selected literature. Unpublished M.Sc. Thesis, University of Alaska. 172 pp..

Crichton, V.F.J.. 1974. Woodland caribou, Lake Winnipeg East. Unpublished Manitoba Department of Mines, Resources and Environmental Management Report. 13 pp..

Cringan, A.T.. 1957. History, food habits and range requirements of the woodland caribou of continental North America. Trans. North Am. Wildlife Conf. 22: 485-501.

Cumming, H.G.. 1975. Clumping behaviour and predation with special reference to caribou. pp. 474-479 in J.P. Luick, P.C. Lent, D.R. Klein and R.G. White (editors). Proceedings of the First International Reindeer and Caribou Symposium. Biological Papers of the University of Alaska, Special Report No. 1 551 pp.

Cumming, H.G. and D.B. Beange. In press. Dispersion of woodland caribou in northern Ontario.

Darby, W.R.. 1978. The seasonal movements and population ecology of woodland caribou (Rangifer tarandus caribou (Gmelin)) in southeastern Manitoba - an interim report with a discussion and recommendations concerning park development. Unpublished University of Manitoba paper. 28 pp..

Darby, W.R. 1979. Seasonal movements, habitat utilization, and population ecology of woodland caribou (Rangifer tarandus caribou (Gmelin)) in the Wallace-Aikens Lake region of southeastern Manitoba. Unpublished M.Sc. Thesis, University of Manitoba. 187 pp..

Dauphiné, T.C. Jr.. 1975. The disappearance of caribou reintroduced to Cape Breton Highlands National Park. Canadian Field-Naturalist, 89 (3): 299-310.

Dauphiné, T.C. 1976. Biology of the Kaminuriak population of barren-ground caribou, Part 4. Growth, reproduction and energy reserves. Can. Wildl. Serv. Rept. Ser. No. 38. 69 pp..

Edmonds, E. J. and M. Bloomfield. 1984. A study of woodland caribou (Rangifer tarandus caribou) in west central Alberta, 1979-1983. Alberta Energy and Natural Resources, Fish and Wildlife Division. 203 pp.

Edwards, R.Y.. 1956. Snow depth and ungulate abundance in the mountains of Western Canada. Journal of Wildlife Management, 20: 159-168.

Eriksson, O.. 1972. Skogskalhyggenas inverkan pa renasnas vinterbete. Prel. rpt. Mimeogr. Inst. of Ecol. Botany. Univ. of Uppsala. 24pp..

Eriksson, O.. 1975. Sylvicultural practices and reindeer grazing in northern Sweden. pp. 108-121 in J.R. Luick, P.C. Lent, D.R. Klein, and R.G. White (editors). Proceedings of the First International Reindeer and Caribou Symposium, Fairbanks, Alaska. 551 pp..

Espmark, Y.. 1970. Abnormal migratory behaviour in Swedish reindeer. Arctic, 23(3): 199-200.

Fuller, T.K. and L.B. Keith. 1981. Woodland caribou population dynamics in northeastern Alberta. Journal of Wildlife Management, 45(1): 197-213.

Gauthier, D.A.. 1984. Population limitation in the Burwash caribou herd, Southwest Yukon. Unpublished Ph.D. Thesis, University of Waterloo. 224 pp..

Hammond, H.L.. 1978. Skid road layout study 1977. Report prepared for B.C. Forest Service, Nelson Forest Region. 126 pp.

Heard, D.C. and S. Boutin. 1982. How an increased effort to kill wolves would benefit caribou populations in the Northwest Territories. Unpublished Report to the Canadian Caribou Management Board. 27 pp.

Holling, C.S.. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomology, 91: 293-320.

Jean, M.. 1981. Biobliographie - Caribou (révision 1980). Gouvernement du Québec, RRF 34, 139 pp..

Karns, P.D.. 1967. Pneumostrongylus tenuis in deer in Minnesota and implications for moose. J. Wildl. Manage. 31(2): 299-303.

Kelsall, J.P.. 1968. The migratory barren-ground caribou of Canada. Canadian Wildlife Service Monograph, No. 3. 340 pp..

Kelsall, J.P.. 1984. Status report on woodland caribou, Rangifer tarandus caribou in Canada in 1982. Unpublished Canadian Wildlife Service Report to the Committee on the Status of Endangered Wildlife in Canada. 99 pp..

Klein, D.R.. 1970. Nutritive quality of Alaskan range forage and associated growth and welfare of reindeer and caribou. Project Completion Report, U.S. Bureau of Land Management, Alaska Cooperative Wildlife Resources Unit, Fairbanks. 29 pp..

Klein, D.R.. 1971. Reaction of reindeer to obstructions and disturbances. Science, 173(3): 393-398.

Klein, D.R.. 1980. Reaction of caribou and reindeer to obstructions - a reassessment. pp. 519-527 in E. Reimers, E. Gaare and S. Skjenneberg (editors). Proceedings of the Second International Reindeer and Caribou Symposium. Roros, Norway. 799 pp..

Klein, D.R.. 1982. Fire, lichens, and caribou. Journal of Range Management, 34(3): 390-395.

Lankester, M.W., Crichton, V.J. and H.R. Timmermann. 1976. A protostrongylid nematode (Strongylida: Protostrongylidae) in woodland caribou (Rangifer tarandus caribou). Canadian Journal of Zoology, 54: 680-684.

Lankester, M.W. and T.H. Northcott. 1979. Elaphostrongylus cervi Cameron 1931 (Nematoda: Metasrongyloidea) in caribou (Rangifer tarandus caribou) of Newfoundland. Canadian Journal of Zoology, 57(7): 1384-1392.

Mahoney, S.P.. 1980. The Grey River caribou herd, May 1979 - May 1980. Unpublished Newfoundland Wildlife Division Report submitted to Newfoundland and Labrador Hydro. 86 pp..

May, R.M.. 1976. Theoretical ecology. Principles and applications. W.B. Saunders (ed.), Philadelphia. 317 pp..

Maynard Smith, J.. 1974. Models in ecology. Cambridge Univ. Press, Cambridge. 146 pp..

Miller, F.L., C. J. Jonkel, and G.D. Tessier. 1972. Group cohesion and leadership response by barren-ground caribou to man-made barriers. Arctic, 25(3): 193-202.

Nieminen, M., P. Vayrynen and R. Vayrynen. 1977. Poron ravitsemusfysiologiasta. (Finnish with English summary). Svomen Luoto 36: 198-101.

Odin, H.. 1971. Effect of clearcutting on climatic factors. Symposium in Ecological Problems of the circumpolar area, June 28-30, Lulea.

Odin, H. and K. Perttu. 1966. Stralnings matningar nava skogsgransen i nossa Sverige. Department of Reforestation, Royal College of Forestry. 24 pp..

Perttu, K.. 1973. The dependence of the forest limit upon different climatological and topographical factors. Department of Reforestation, Royal College of Forestry.

Poole, R.W.. 1974. An introduction to quantitative ecology. McGraw-Hill, New York. 532 pp..

Porter, T.. 1983. 1982 fall migration of Mount Peyton Caribou. Unpublished Newfoundland Wildlife Division Report. 43 pp..

Raven, P.H. and H. Curtis, 1970. Biology of Plants. Worth Publishers, pp. 412-415.

Roby, D.D.. 1978. Behavioural patterns of barren-ground caribou of the central arctic herd adjacent to the Trans. Alaska oil pipeline. Unpublished M.Sc. Thesis, University of Alaska, Fairbanks. 250 pp..

Rodhe, B.. 1965. Redogorelse for undersokningar av snoforhallanden kring. Messauve damningsomrade 1958-1962. SmHl, Klimatbyran, Stockholm. 60 pp..

Salo, L.J.. 1975. Silvicultural practices and reindeer grazing in northern Sweden. pp. 420-422 in J.R. Luick, P.C. Lent, D.R. Klein, and R.G. White (editors). Proceedings of First International Reindeer and Caribou Symposium. Biological Papers of the University of Alaska. Special Report No. 1. 551 pp..

Schraeder, H.. 1982. A discussion on the effects of logging on woodland caribou (Rangifer tarandus caribou) with specific inference to the Armstrong airport herd. Unpublished Ontario Ministry of Natural Resources Report. 21 pp.

Shoesmith, M.W.. 1978. Social organization of wapiti and woodland caribou. Unpublished Ph.D. Thesis, University of Manitoba. 155 pp..

Simkin, D.W.. 1965. A preliminary report of the woodland caribou study in Ontario. Unpublished Ontario Department of Lands and Forests Reports, No. 59. 76 pp..

Skoog, R.O.. 1968. Ecology of the caribou (Rangifer tarandus granti) in Alaska. Unpublished Ph.D. Thesis, University of California (Berkeley). 720 pp..

Stardom, R.R.P.. 1975. Woodland caribou and snow conditions in southeast Manitoba. pp. 436-461 in J.R. Luick, P.C. Lent, D.R. Klein, and R.G. White (editors). Proceedings of the First International Reindeer and Caribou Symposium. Biological Papers of the University of Alaska, Special Report No. 1. 551 pp..

Stardom, R.R.P.. 1977. A study of the winter ecology of woodland caribou, Rangifer tarandus caribou, and comparison with some aspects of the winter ecology of moose, Alces alces andersoni, and whitetail deer, Odocoileus virginianus dacotensis (Mammalia: Cervidae), in southeastern Manitoba. Unpublished M.Sc. Thesis, University of Manitoba. 147 pp..

Storey, D.R. and K.M. Storey. 1980. Woodland caribou habitat evaluation - a score sheet method (revised). Unpublished Manitoba Department of Renewable Resources and Transportation Services Research Report, No. 80-24. 23 pp..

Telfer, E.S.. 1974. Logging as a factor in wildlife ecology in the boreal forest. The Forestry Chronicle, October. 186-190.

Theberge, J.B. and D.A. Gauthier. 1985. Models of wolf-ungulate relationships: when is wolf control justified? Wildl. Soc. Bull. 13(4):449-458.

Thomson, B.R.. 1977. The behaviour of wild reindeer in Norway. Ph.D. Thesis, Univ. of Edinburgh, Scotland.

Trainer, D.O.. 1973. Caribou mortality due to the meningeal worm (Parelaphostrongylus tenuis). Journal of Wildlife Management, 9: 376-378.